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PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTONA RECLASSIFICATION OF *IRIS* SPECIES BEARING
ARILLATE SEEDS

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In his revision of the genus *Iris* L., Rodionenko (1961) placed in the subgenus *Iris* only those species with aggregations of multicellular hairs (beards) on the outer perianth segments. Beardless rhizomatous and nonrhizomatous species were placed in other subgenera, or were transferred to genera other than *Iris*. In his system, subgenus *Iris* consisted of section *Hexapogon* emended to include all species with arillate seeds, and section *Iris* containing the remaining non-arillate species. *Hexapogon* consisted of the subsections *Regelia*, *Pseudoregelia* and *Oncocyclus*. *Regelia*, however, had the same circumscription as subsection *Hexapogon* (Bunge) Bentham *emend.* Lawrence (1953), and Rodionenko's use of the name *Regelia* was superfluous (see also under section *Hexapogon* below).

Data published since the Rodionenko revision of the genus make even more obvious the heterogeneous nature of subsection *Hexapogon* (Bunge) Bentham *emend.* Lawrence and its synonym *Regelia* (Dykes) Rodionenko. The following new system for the arillate species in *Hexapogon* is proposed.

Iris subgenus *Iris*

Section *Iris* (This type section of the subgenus lacks arillate species.)

Section *Hexapogon* (Bunge) Baker

Section *Regelia* Lynch

Section *Oncocyclus* (Siemssen) Baker

Section *Psammiris* (Spach) J. Taylor

Section *Pseudoregelia* Dykes

The essential features of this reclassification are (1) the segregation of species previously included in section *Hexapogon* (Bunge) Baker *emend.* Rodionenko (1961) into five distinct taxa, and (2) the designation of a type of the section *Regelia* Lynch. A compendium of literature relevant to section *Iris* is also included.

Iris subgenus *Iris*

Iris sect. *Pogiris* Tausch in Hort. Canalius, 1 (1823); *idem* in Schultes Additamentum Mantissum, 2:369 (1824), *quoad typus*.—*Iris* subgen. *Euiris* Alefeld in Bot. Zeit., 21:296 (1863), *p.p.*; *non* Boissier Fl. Orient., 5:118 (1884); *non* Klatt in Linnaea, 33:591–604 (1866).—*Iris* sect. *Euiris* Bentham in Bentham and Hooker, Gen. Pl., 3:687 (1882).—*Iris* sect. *Pogiris* Tausch *emend.* Lawrence in Gent. Herb., 8(4):353 (1953).—*Iris* sect. *Iris* *emend.* Lawrence in Gard. Irises, 142 (1959).

Type of the subgenus: *I. germanica* L.

Species composing subgenus *Iris* are characterized by distinctly rhizomatous stems, and flowers with beards of multicellular hairs on the outer, and occasionally the inner, perianth segments.

KEY TO THE SECTIONS OF SUBGENUS *IRIS*

1. Seed without an aril; capsule usually dehiscent very near apex, but if dehiscent considerably below apex, then some internal placentation ruptured at maturity Section *Iris*
1. Seed with conspicuous creamy-white aril; capsule dehiscent subapically or laterally; mature placentation intact 2
2. Both inner and outer perianth segments with conspicuous more or less linear beards 3
3. Spathe valves (bracts) 3 or 4; rhizome usually compact, slowly creeping; seed with small aril; chromosome number of counted species: $n = 9$ Section *Hexapogon*
3. Spathe valves 2; rhizome stoloniferous, readily spreading; seed with large aril; chromosome number of counted species $n = 11$ Section *Regelia*
2. Only outer perianth segments bearded, or if all segments bearded, then beards on outer segments scattered 4
4. Beard on outer segments scattered; spathe 1-flowered; seed with large aril Section *Oncocyclus*
4. Beard on outer segments linear; spathe usually 2-flowered; seed with aril much smaller than seed 5
5. Rhizome creeping or spreading by stolons; flowers essentially monochromic though sometimes lightly veined Section *Psammiris*

5. Rhizome compact, gnarled; flowers usually dichromic, spotted
 ----- Section *Pseudoregelia*

Iris section *Iris*

Iris subgen. *Pogiris* Tausch, *l.c.*; *idem* in Schultes, *l.c.*—*Iris* subgen. *Pogoniris* Spach in Ann. Sci. Nat. ser. 3, 5:103 (1846); *idem* in Hist. Nat. Veg., 13:48–68 (1846), *p.p.*; Klatt in Bot. Zeit., 30:515 (1872), *p.p.*; Baker in Journ. Linn. Soc. Lon. Bot., 16:143 (1877), *p.p.*; Randolph in Bull. Amer. Iris Soc., 109:4 (1948), *p.p.*—*Iris* subgen. *Euiris* Alefeld in Bot. Zeit., 21:296 (1863), *p.p.*; *non* Boissier, *l.c.*; *non* Klatt, *l.c.*—*Iris* subsect. *Pogoniris* (Spach) Bentham in Bentham and Hooker, *l.c.*; Pax in Engler and Prantl, Nat. Pflanzenfam., 2(5):145 (1888), *p.p.*; Lawrence, *l.c.*—*Iris* sect. *Pogoniris* Baker, *l.c.*, *p.p.*—*Iris* subgen. *Eupogoniris* Randolph, *l.c.*

Type of the section: *I. germanica* L.

In his reclassification of *Iris*, Lawrence (1953, 1959) divided subsection *Pogoniris* into the series *Pumilae* and *Elatae*. To the former were assigned those species which are less than 3 dm tall, and either acaulescent or if caulescent, then not branched. Series *Elatae* comprised the taller species which are distinctly caulescent and branched. Although he cited these taxa, Rodionenko did not include them in his system.

Recent collections of bearded irises have included forms which could justify emending series *Pumilae* to include the low-growing species which are nevertheless caulescent and branched, e.g., *I. furcata* MB, *I. timofejewii* Woron., and perhaps others. Anyone systematically treating these non-arillate species should include such emendation if the taxon is retained.

Because of the numerous morphological, karyological, genetic and distributional differences between the arillate and the non-arillate species, Rodionenko (1961) removed arillate species from section *Iris*, based on *I. germanica* L., and gave them sectional rank collectively in *Hexapogon*. His circumscription of section *Iris* is retained here.

Iris section *Hexapogon* (Bunge) Baker in Gard. Chron. ser. 3, 5:787–788 (1876); Boissier, Fl. Orient., 5:119 (1884).

Iris subgen. *Hexapogon* Bunge *ex* Alefeld in Bot. Zeit., 21:296 (1863), *nom. illegit.*; Baker in Journ. Linn. Soc. Lon. Bot., 16:147 (1877), *nom. illegit.*—*Iris* subsect. *Hexapogon* (Bunge) Bentham in Bentham and Hooker, Gen. Pl., 3:687 (1882); Pax in Engler and Prantl, Nat. Pflanzenfam., 2(5):145 (1888).

Type of the section: *I. falcifolia* Bunge.

Species included within the section:

- I. falcifolia* Bunge 1847
- I. longiscapa* Ledebour 1853

The name *Hexapogon*, first used by Bunge (1847) in describing the new species *I. falcifolia* and *I. filifolia* Bunge (an invalid synonym of *I. longiscapa* Ledeb.), was taken up by Alefeld (1863) for a subgenus circumscribing the two Bunge species and *I. susiana* L. Because *I. susiana* was the type for Spach's earlier subgenus *Susiana* (1846), Alefeld's use of *Hexapogon* was illegitimate (Article 63, International Code of Botanical Nomenclature (ICBN), 1969). Baker (1876) transferred *I. susiana* to section *Oncocyclus* and first validly published *Hexapogon* as a section comprising *I. falcifolia* and *I. filifolia* Bunge only. (The following year (1877) he raised *Hexapogon* to the rank of subgenus, but his use of the name at that rank was illegitimate (Article 64, ICBN).)

In 1892, Baker transferred the *Hexapogon* species to subgenus *Pogoniris*, and introduced the name *Regelia* for a subgenus containing three species described by Eduard Regel. Although it is apparent that Baker intended to segregate *Regelia* from *Hexapogon* and *Pogoniris*, he did not adequately characterize *Regelia*, and it remained a *nomen nudum* until validly published as a section by Lynch in 1904. A type was not designated.

Dykes considered *I. falcifolia* and *I. filifolia* Bunge to be synonymous, and transferred them (1913) from *Pogoniris* to section *Regelia*. Because one or the other of these *Hexapogon* species must be considered the type for the earlier section *Hexapogon* (Bunge) Baker, Dykes' use of the name *Regelia* was illegitimate (Article 63, ICBN). Rodionenko's use of *Regelia* for a subsection (1961) was illegitimate for the same reason. Lawrence did not acknowledge section *Regelia* Lynch, and combined *Regelia* Dykes, including *Hexapogon*, with *Psammiris* species in subsection *Hexapogon* (1953, 1959).

I. falcifolia and *I. longiscapa* are xeritic species of the Turkmenian and Uzbekian deserts in southcentral U.S.S.R., and of a few similar but restricted localities in Iran and Afghanistan. They are characterized by weakly or non-stoloniferous rhizomes, very narrow leaves, thin and leafless stems, and spathes of 3 or 4 bracts enclosing 2 to 5 small flowers with all perianth segments bearded. *Iris longiscapa* has been examined karyologically (Randolph and Mitra, 1961), and is the only bearded iris species yet counted with the diploid chromosome number 18.

Iris section *Regelia* Lynch, Bk. *Iris*, 56 (1904); Fedtschenko in Komarov, Fl. USSR, 4:539 (1935); *nec* Dykes, Gen. *Iris*, 123 (1913), *p.p.*, *nom. illegit.*

Iris subgen. *Regelia* M. Foster *ex* Baker, Handbk. *Irideae*, 1 (1892), *p.p.*, *nom. nudum*.—*Iris* subgen. *Pogoniris* Randolph in Bull. Amer. Iris Soc., 109:4 (1948), *p.p. affin. sect. Regelia* Lynch; *non* Spach (1846), *l.c.*; *non* Baker (1876), *l.c.*—*Iris* subsect. *Regelia* (Dykes) Rodionenko, Gen. *Iris* L., 198–199 (1961), *p.p.*, *nom. illegit.*

Type of the section: *I. korolkowii* Regel.

Species included within the section:

- I. afghanica* Wendelbo 1972
- I. darwasica* Regel 1884
- I. heweri* Grey-Wilson & Mathew 1974
- I. hoogiana* Dykes 1916
- I. korolkowii* Regel 1873
- I. kuschensis* Grey-Wilson & Mathew, ? *edit.*
- I. lineata* M. Foster 1887
- I. stolonifera* Maximowicz 1880

To my present knowledge, a type of section *Regelia* as circumscribed by Lynch has not previously been designated. After a study of that author's protologue, and in an attempt to preserve both the originally intended and the current usage of *Regelia* (Article 7 B, ICBN), I have selected and here designated *I. korolkowii* Regel as the type of this section.

The *Regelia* species are essentially montane species characterized by more or less stoloniferous rhizomes bearing unbranched scapes each with a 2-bracted spathe containing 2 (rarely 3) flowers with all perianth segments bearded. They differ from all other arillate sections except *Oncocyclus*, with which they show the greatest affinity, in general distribution, plant habit, spathe and/or floral morphology, and, except for chromosome number in *Psammiris* and *Pseudoregelia*, in karyotype. Intersectional hybrids between *Regelia* and the remaining arillate sections (except *Oncocyclus*) have been difficult or impossible to obtain. The rare hybrids produced have been sterile.

In contrast, there is marked fertility in intersectional diploid hybrids between *Regelia* and *Oncocyclus*, and, excepting the large metacentric chromosome of *Regelia* species, a striking similarity of haploid karyotypes in the two sections. The taxa are differentiated, however, by the weakly or non-stoloniferous rhizomes, 1-flowered spathes, and widely scattered beards on the outer perianth segments of *Oncocyclus* species.

Iris section *Oncocyclus* (Siemssen) Baker in Gard. Chron. ser. 3, 5:788 (1876).

Oncocyclus Siemssen in Bot. Zeit., 4:706-707 (1846).—*Iris* subgen. *Susiana* Spach in Ann. Sci. Nat. ser. 3, 5:110 (1846); *idem* in Hist. Nat. Veg., 13:70-71 (1846).—*Iris* subgen. *Oncocyclus* (Siemssen) Alefeld in Bot. Zeit., 21:296 (1863); Baker in Journ. Linn. Soc. Lon. Bot., 16:142 (1877).—*Iris* subsect. *Oncocyclus* (Siemssen) Benthall (1882), *l.c.*; Pax (1888), *l.c.*—*Iris* subgen. *Pogoniris* Randolph in Bull. Amer. Iris Soc., 109:4 (1948), *p.p. affin. gen. Oncocyclus* Siemssen; *non* Spach (1846), *l.c.*; *non* Baker (1876), *l.c.*

Type of the section: *I. paradoxa* Steven.

Species included within the section:

- I. acutiloba* C. A. Meyer 1831
- I. antilibanotica* Dinsmore 1933
- I. atrofusca* Baker 1894
- I. atropurpurea* Baker 1889
- I. auranitica* Dinsmore 1933
- I. barnumiae* M. Foster & Baker 1888
- I. biggeri* Dinsmore 1933
- I. bismarckiana* (Dammann) Regel 1890
- I. bostrensis* Mouterde 1954
- I. camillae* Grossheim 1950
- I. calcaria* Dinsmore *inedit.*
- I. cedretii* Dinsmore *ex* Chaudhary 1972
- I. damascena* Mouterde 1967
- I. demawendica* Bornmueller 1902
- I. ewbankiana* M. Foster 1901
- I. gatesii* M. Foster 1890
- I. grossheimii* Woronov 1928, ? *hyb. nat.*
- I. hauranensis* Dinsmore 1933
- I. haynei* (Baker) Mallet 1904
- I. heylandiana* Boissier & Reuter 1877
- I. hermona* Dinsmore 1933
- I. iberica* Hoffmann 1808
- I. kirkwoodii* Chaudhary 1972
- I. lineolata* (Trautvetter) Grossheim 1950
- I. lortetii* Barbey 1881
- I. lupina* M. Foster 1887
- I. lycotis* Woronov 1915
- I. maculata* Baker 1876
- I. manissadjanii* Freyn 1896
- I. meda* Stapf 1885
- I. nigricans* Dinsmore 1933
- I. paradoxa* Steven 1844
- I. petrana* Dinsmore 1933
- I. polakii* Stapf 1885, *p.p.*
- I. sari* Schott 1876
- I. schelkownikowii* Fomin 1907, ? *hyb. nat.*
- I. schischkinii* Grossheim 1950
- I. sofarana* M. Foster 1899
- I. sprengeri* Siehe 1904
- I. susiana* Linnaeus 1753
- I. urmiensis* Hoog 1900
- I. yebrudii* Dinsmore *ex* Chaudhary 1972

Of the arillate irises, the section *Oncocyclus* is the most refractory to systematic treatment. The situation has resulted from the numerous intraspecific phenotypic variations among populations and collections

of apparently valid species, the frequency of natural hybridization among sympatric species and the use of specific epithets for hybrids and their nothomorphs, and variations in interpretation and use of differentiating criteria among taxonomists. It is possible, therefore, that the list immediately above lacks the names of valid *Oncocyclus* species, and includes names which may be synonymous with others. It should be considered a tentative listing in lieu of more thorough examinations of putative species and hybrids, and of systematic analyses based on characteristics perhaps somewhat more instructive of this section than gross morphology and habitat alone.

The *Oncocyclus* species are found in dry desert and montane habitats from the eastern Mediterranean coastal region east and northeast into Iran, Afghanistan and Turkmenian U.S.S.R. They are characterized by weakly or non-stoloniferous rhizomes, more or less falcate radical leaves, and a scape bearing a 2-bracted spathe containing a single flower. Both inner and outer perianth segments vary remarkably in outline among the species, from the much reduced sepals of *I. paradoxa*, the type for the section, to the narrow and acutely pointed segments of the *I. meda*-*I. acutiloba* complex and the wide rounded perianth of *I. susiana* and similar cultivated species. All, however, possess a beard of multicellular hairs scattered widely and often densely along the haft and onto the blade of the sepal.

Iris section *Psammiris* (Spach) Taylor *comb. nov.*

Iris subgen. *Psammiris* Spach in Ann. Sci. Nat. ser. 3, 5:110 (1846); *idem* in Hist. Nat. Veg., 8:69-70 (1846).

Type of the section: *I. humilis* Georgi.

Species included within the section:

I. bloudowii Bunge *ex* Ledebour 1833

I. humilis Georgi 1775

? *I. mandshurtica* Maximowicz 1880

I. potaninii Maximowicz 1880

Because there has been some reluctance to reject *I. flavissima* Pallas as a later synonym for *I. humilis* Georgi, a brief nomenclatural history of this species is included here.

Messerschmidt found a low-growing yellow iris near the Transbaikalian town of Ulan-Ude. Its description ("Iris humilis angustifolia. . . .") was first published by Ammann (1739) after number 133, page 101.

Gmelin (1747) described after his number 31 "iris foliis ensiformibus, caule bifloro. Tab. V. Fig. 2" and included as a synonym "Iris humilis angustifolia. . . . Mess. Amm. (Stirp. rar.) Ruth. post 133." Gmelin stated that his number 31 (as *Ammanni*) had also been observed by Messerschmidt in the hills near Ulan-Ude. It is obvious that Gmelin considered his number 31 to be the same as Messerschmidt-Ammann number 133.

Georgi (1775) again observed the iris in the southern Baikal region, and published the following description of it under the name *I. humilis*: "Iris humilis, angustifolia, lutea. Messerm. Amman. (Stirp. rar.) p. 101. Radix flavo alba fibrosa. Caulis 3. ad 6. pollicum, saepius biflorus, foliis gramineis, duplo longioribus." It is apparent that Georgi considered his *I. humilis* to be the same as Messerschmidt-Ammann number 133 (the only "iris humilis angustifolia" on page 101), and his diagnosis is compatible with Gmelin's figure 2, plate V.

In 1776, Pallas published the name *I. flavissima*, and included as a synonym: "Iris foliis ensiformibus. . . . Gmel. Flor. Sibr. I. p. 31. tab. V. fig. 2. cum synon. Ammanni." Thus *I. flavissima* is the same as Gmelin number 31 and therefore Messerschmidt-Ammann number 133, and *I. humilis* Georgi, also conspecific with the latter, is the first validly published name for this species.

Spach (1846) first published *Psammiris* as a monospecific subgenus based on *I. arenaria* Waldst. & Kit., a later synonym of *I. humilis* Georgi. Baker (1877) later combined psammirises with *Pogoniris*, where they remained until Lawrence (1953) transferred them to subsection *Hexapogon*. Although most forms of *I. humilis* have more or less stoloniferous rhizomes and radical leaves which are tinged with anthocyanin pigments at vernal emergence (characteristics sometimes assumed to show affinity with common garden forms of some *Regelia* species), the psammirises differ from other arillate species in karyotype, general distribution range, plant habit and/or floral and rhizome morphology.

The psammiris karyotype (Simonet, 1934; Gustafsson and Wendelbo, 1975) is quite distinct among arillate irises, unlike even those of *Regelia* and *Pseudoregelia* species with similar chromosome numbers (Randolph and Mitra, 1961; Zakhariyeva and Makushenko, 1969). The few intersectional hybrids produced experimentally between *Psammiris* and other arillate species are sterile.

Psammirises are found in open meadows and on hillsides from south-central Europe east into transcaucasian U.S.S.R., and on exposed mountain slopes and in grasslands and shaded, dry mountain valleys from the western Altai region north and east into Mongolia, Manchuria and transbaikalian U.S.S.R. They are the most widely distributed of the arillate species, and the only arillate irises native to central Europe.

Although there are some differences in flower stalk length and rhizome morphology among *Psammiris* species and geographical forms of species, all produce narrow radical leaves which frequently dry to leave fibrous vestiges near the rhizome, and thin scapes bearing 1 or 2 2-bracted spathes each with 1 or 2 short-lived flowers with more or less elongated perianth tubes. The withering flowers become characteristically helically twisted (Spach, 1846; Ugrinsky, 1922).

Iris section *Pseudoregelia* Dykes, Gen. Iris, 129 (1913).

Iris subgen. *Pseudoevansia* Baker, Hndbk. Irideae, 2 (1892), *nom. nudum*.—*Iris* sect. *Pseudoevansia* Lynch, Bk. Iris, 55 (1904), *nom.*

nudum.—*Iris* subsect. *Pseudoregelia* (Dykes) Lawrence in *Gent. Herb.*, 8(4):356 (1953); Rodionenko, *Gen. Iris L.*, 199 (1961).

Type of the section: *I. kamaonensis* Wallich ex D. Don.

Species included within the section:

- I. goniocarpa* Baker 1876
- I. hookerana* M. Foster 1887
- I. kamaonensis* Wallich ex D. Don 1841
- ?*I. leptophylla* Lingelsheim 1922
- I. sikkimensis* Dykes 1908, ? *hyb. nat.*
- I. tigridia* Bunge ex Ledebour 1829

Baker (1892) created the subgenus *Pseudoevansia* to include several small central Asian species which he believed were related to the crested *Evansia* species. His differential diagnosis was based exclusively on the rudimentary crests terminating the beard of pseudoevansias, structures now known to have little taxonomic significance. Lynch (1904) retained *Pseudoevansia* as a section, but failed to describe the taxon further. The name remained a *nomen nudum*. Dykes (1913) examined *Pseudoevansia*, transferred some included species to other taxa, and fully characterized and published the name *Pseudoregelia* as a section circumscribing the remaining species. Both Lawrence (1953, 1959) and Rodionenko (1961) retained the name for a subsection with the same circumscription.

The pseudoregelias are essentially montane often alpine species found from the Indian Himalayas north and east into Nepal, Tibet, Mongolia and eastern Siberia, and west into the Altai region. They superficially resemble *Psammiris* species in dwarf plant habit and floral morphology, but differ significantly in rhizome morphology and in karyotype (Simonet, 1952). The known *Pseudoregelia* species exhibit no close affinities with other arillate irises. Fertile intersectional hybrids involving pseudoregelias have not been produced.

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